MATE LOCATION STRATEGIES IN THE WALL BROWN BUTTERFLY, *LASIOMMATA MEGERA* (L.) (LEPIDOPTERA: SATYRIDAE): WAIT OR SEEK?

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Introduction

Male butterflies are generally described as adopting one of two alternative strategies in the process of locating mates; perching, or waiting for them, and patrolling, or actively seeking them in flight (Scott 1974, Shields 1967; Shreeves 1980).

Characteristic sites varying in surface, height and situation, are selected by perchers, where they bask in the sun, and from these they launch themselves at passing insects (cf., Baker (1972) for *I. io* (L.) and *A. urticae* (L.); Davies (1978) for *P. aegeria* (L.); Joy (1902) for *A. iris* (L.) and Peachey (1980) for several species, particularly *H. lucina* (L.)). Distinctions, in height, habitat and speed, also occur for patrolling species as evident from studies of *A. cardamines* (L.) (Wiklund and Ahrberg 1978; Courtney 1980; Dennis in press); *L. sinapis* (L.) (Wiklund 1977, Peachey 1980; Warren 1981); *M. galathea* (L.) and *B. euphrosyne* (L.) (Peachey 1980).

Baker (1972) has argued that the tendency to 'stay put' or perch is the result of some female requirement, for instance nectar sources or oviposition sites, being concentrated; moreover, perching has been likened to territoriality (cf., Davies 1978) in as much as the area is defended, resident males typically intercepting and leading intruders out of the area. Baker extends the argument by pointing out that perching necessarily evolves where the energy used in defence is less than the energy used in patrolling. It follows then that the number of butterflies perching is a measure of the magnitude and concentration of a resource(s) in a particular environment though Baker conceded that the territory: male ratio determines the tendency to share spots as opposed to keep searching, via a raising of the territoriality threshold.

For only one British species have both mate location strategies been noted, – *P. aegeria* (Davies 1978). While some males are perching in woodland clearings, others have been observed patrolling in the canopy. Investigating potential mates and attempted courtships in the canopy identifies the activity as patrolling; – they are not merely waiting their turn for clearing perches. Patrolling in *A. urticae* and *I. io* was not made explicit by Baker, but as mate location is the reason for establishing territories, searching for the latter cannot be easily separated from the former and it implies that both butterflies do engage in patrolling, even if this is enforced.

Davies also discovered behaviour to vary. On sunny days, detailed experiments show there to be a premium on perching sites. Females are more abundant in clearings, and size of sun spot and time of day determine the number of males found there. On

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overcast days, the butterfly patrols regardless of location. Virtual lack of skirmishing points to abandonment of territories, yet the butterfly still attempts to court. As for *A. urticae*, Davies has recognised the readiness of *P. aegeria* males to accept intruders but has been able to link this closely with clearing size.

The present paper explores some comparative data on the closely related Wall Brown butterfly, *L. megera*. This butterfly is a known percher, but does it also patrol? Where does it perch and why are two of a series of related questions, but the emphasis is placed on examining how flexible mate location behaviour can be?

Materials and methods

The study has been conducted mainly at Brereton Heath near Congleton, but also along the Bollin valley, in north Cheshire. Individual behaviour has been determined using a cassette recorder and by making direct observations on seriation in activites and on specific lines of movement. Behaviour and movement over a wider area and on a number of individuals in succession has been conducted using transect (Pollard 1977; 1979) and capture, mark, release, recapture (CMRR) (Ehrlich and Davidson 1960) techniques separately and together.

Behaviour has been reduced to a number of simple categories (specifically flight, feeding, resting, basking, skirmishing, courtship and inspection) to avoid making premature judgements on various activities. Numerical techniques applied to timed activities, – specifically the calculation of behavioural 'distances' (E^2 of Edwards (1971)), least space analysis (Coxon and Davies 1980) and cluster analysis (Sneath and Sokal 1973), – have been used in an attempt to distinguish perchers from patrollers.

Results

A simplified tabulation of timed behaviour (Table 1) shows that males spend much of their time basking or resting. When basking the wings are open and angled to the sun and on landing the butterfly usually orientates itself accurately and quickly. The wings are closed during rest. Different surfaces are chosen for these activities (Table 2) but preference is for bare ground along paths, though other topographically distinctive surfaces are selected even newly constructed ranch fencing. Feeding and flight occupy much the same length of time.

	SF	LF	F	BR	SK	I
Total Time (seconds)	298.5	2241.5	1984	8765	584	83.5
Number of observations	132	187	153	162	115	67
Percent of total observation time for all activities	2	16	14	63	4	1

Table 1 Timed activities for *L. megera* males on Brereton Heath during 1981. Symbols as for Figure 1. Total observation time = 3 hrs 53 minutes.

Long flights are generally less than a metre above the ground, but vary according to the surface and are much less for low ground cover. Flights are usually fast, zig-zagging, often circular and typically investigative covering a wide area. Some are brief transects or circuits; others are more directional and long distance movements representing voluntary displacement and change of location.

	Year	
Surface	1981	1982
Path; bare ground	123	45
Grass	5	3
Flowerheads	0	6
Leaves of herbs, i.e. dock and nettle	3	15
Stones, bricks	4	2
Leaves of bushes, saplings and bramble	0	5
Fence posts and bars	0	18
Paper, tin, etc.	1	1
Mossy ground	2	0

Table 2 Sample data on basking and resting (perching) sites adopted by *L. megera* males on Brereton Heath in 1981 and 1982.

Males are continually scanning on the wing, but stop to inspect a wide range of objects apart from flowers. Skirmishing and attempted courtships take place while the butterfly is in flight as well as when basking and resting. Male *L. megera* skirmish with a variety of insects (Table 3); most other male *L. megera* induce much longer interactions varying from short spiral flights lasting 2 or 3 seconds to higher and extended spirals and dives described by Baker for *A. urticae* and *I. io*. Attempted courtships with female *L. megera* are longer affairs (average 35 seconds) and involve distinctive behaviour (Dennis in prep).

Insect	Frequency	Average time	(seconds)
L. megera (females)	14	34.7	
L. megera (males)	27	9.3	* *O. venata* (Br & Gr)
M. jurtina (females)	5	9.0	*L. phlaeas* (L.)
Bees and wasps	7	1.9	*P. brassicae* (L.)
Dragonflies	13	2.2	*A. napi* (L.)
Other butterflies*	17	2.1	*A. urticae* (L.)
			I. io (L.)

Table 3 Frequency and average time of attempted courtships and skirmishing of *L. megera* males with other insects on Brereton Heath in 1981.

Seriation in behaviour (Figure 1) based on a sample of males emphasises the association of different activities and modes of behaviour. Typical is a feeding mode of regular but short sessions on flowerheads separated by 'hops' or short flights from one flower to another. More significantly the diagram underlines the role of long flights and basking. Skirmishing and courtship are associated with both and males continually investigate in flight; together, this confirms the objective of basking as 'perching' and long flights

as 'patrolling'. This average picture also demonstrates the functional interdependence of basking and long flight, a deduction which seems at odds with more casual observations of 'pure' behaviour of 'perching' and voluntary displacement respectively.

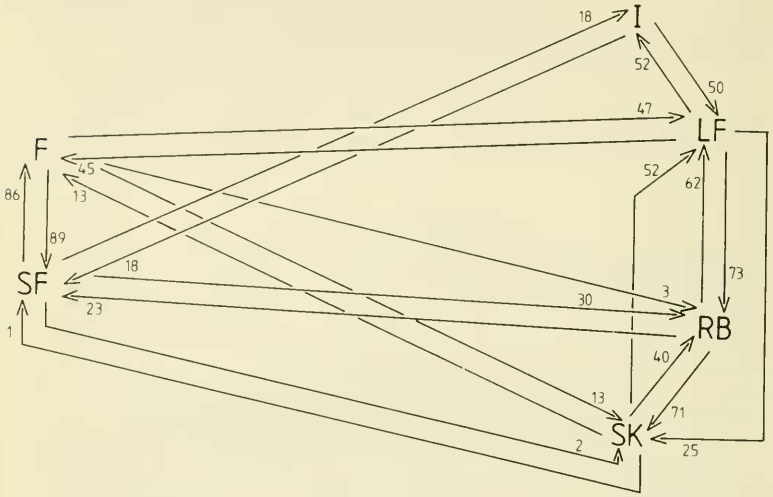

Figure 1 Seriation in male *L. megera* behaviour (n = 30), June and August 1981. F = feed from flower, I = inspect, SF = short flight; LF = long flight; RB = resting or basking; SK = skirmishing and attempted courtship. Short flight denotes rapid transitions of activity, whereas long flights revealed searching and investigative behaviour. Halts in flight only are counted as inspections.

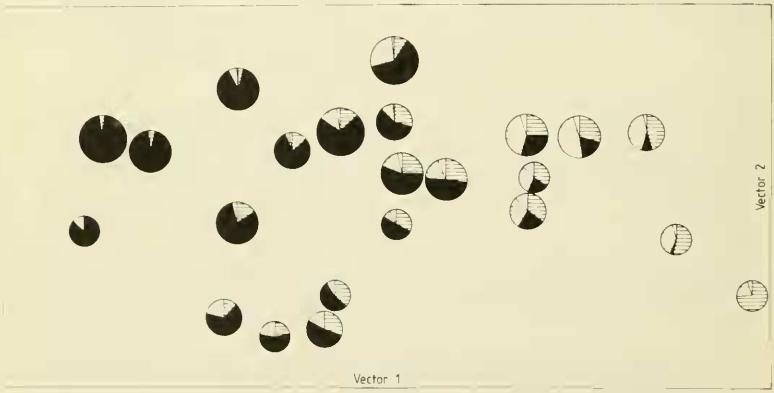

Figure 2 A computer map (non-metric 2 dimensional scaling plot) of distances (Edward's E^2) between 23 male *L. megera* based on timed activity. Shading = flights; black = basking/resting; stipple = feeding; white = skirmishing, inspection and courtship. Four sizes of circle represent observation time (minutes):- <300; 300 – 500; 500 – 1000; > 1000. Kruskal's stress for the computer plot is 3.9%.

Figure 2 summarises individual behaviour. Three groups of individuals are suggested by maximum linkage clustering but this is not confirmed in the non-metric scaling plot nor by single link clustering. In effect, the array describes a continuum from extremes of perching (basking and skirmishing non-feeders in the main) to patrolling (flying and skirmishing feeders). Intermediate behaviours also occur, that they are not an artefact of the observation period or switches in behaviour is confirmed by time-scaled plots.

Extremes of behaviour and intermediate forms have been monitored and mapped. Confinement of males to small areas, 'territories', is not limited to the perching mode. More varied behaviour involving longer feeding episodes and extensive patrolling circuits has similarly been identified with definite areas – a neat example was provided by a narrow fenced path, some 100 metres in extent, between a barley and ley grass field on Alderly Edge, along which three males patrolled back and forth. On these occasions skirmishing is less demonstrative, no real attempt being made to lead an 'intruder' out of the zone. Yet, extreme perching behaviour is not devoid of voluntary shifts in perching site and inspection tours. For example, of 27 'sorties' effected by one male from a small gravel heap over a 45 minute period, 11 appeared to be unrelated to intruders and involved slower, low inspection flight. At the other extreme, males 'passing through' territories have been observed to undergo long, fast but investigative flights, apparently 'domainless'.

CMRR work demonstrated that male *L. megera* have a propensity to stay in the same location, some throughout a day, others over several days (Dennis, in prep). On the other hand, territories also change hands readily but retain much the same number of individuals. In north Cheshire, males select linear habitats for perching and patrolling, such are hedgerows – despite the crop in the field – roadsides, tracks and paths, bank margins to lakes, even the new lines of ranch fencing recently constructed. The latter has provided some valuable insights into behaviour; more males roost under the horizontal bars of the fence than patrol or perch along its edges at any one time, confirming casual observations of regular spacing for mate location along uniform habitats, such as roadsides, though CMRR work failed to locate precise territorial boundaries in such habitats. Perching and patrolling zones have also been found to be oviposition sites and thus sites of female emergence (Dennis, in prep), the eggs being laid in grass curtains fronting hedges, fences and bushes and recesses along banks.

The frequency of males and females drops significantly over uniform open spaces and those seen are generally moving rapidly in straight lines; however, not all linear habitats are used. Males congregate in sheltered sunny spots, avoiding shade and areas exposed to wind.

Transect data records much the same proportion of basking and long flights from 9.00 am to roosting time (Table 4). The implication is that perching and patrolling occur throughout the day, confirming other observations. A greater inclination to perching is

	Time of day								
	9-10	10-11	11-12	12-1	1-2	2-3	3-4	4-5	5-6
Percent basking	34.2	30.8	26.9	30.5	31.3	39.0	29.3	26.6	52.4
Percent long flight	34.2	33.9	37.3	40.7	43.8	29.3	39.0	25.0	33.3
Percent feeding	14.5	18.5	23.9	18.6	12.5	17.1	19.5	21.9	9.5
Number of separate observations	76	65	67	59	32	41	41	64	21

Table 4 Percentage of basking/resting, long flights and feeding for male *L. megera* during transect counts on Brereton Heath in August 1982.

suggested in the morning and evening and to patrolling around midday. Proportions of patrollers and perchers also vary from day to day subject to the weather. Precise conditions have not been monitored but remarkable uniformity occurs in the percent of perchers on overcast days (55% – 58%; n = 4) compared to bright, cloudless, sunny conditions (12%, 31%; n = 2). This is a reversal of observations made on *P. aegeria* and may reflect sensitivity to movement in a linear habitat when energy levels are high. Proportions of patrollers and perchers no doubt changes over a longer time span in response to environmental changes. A number of perching spots were lost in 1982 due mainly to the provision of parking and other recreational facilities on the heath; however, one small area succumbed to vegetation succession.

Discussion

L. megera is a percher and patroller. In the process of obtaining mates, it displays a wide range of behaviour between the extremes of territorial defence and more passive acceptance of competitors while scanning the ground in flight. There is evidence too that we should expect variation in behaviour at the population level, – in respect of habitat differences and population density – within populations, – due to seasonal circumstances including habitat changes, weather and light conditions – and perhaps even at the individual level, – linked to insect age and inherited bias. All this points to the existence of a flexible response system and much additional work needs to be done on this aspect of mate location.

By extension, we should also expect to find variation in mate location behaviour among other butterflies, and because this reflects upon their habitats and other adaptations, there is a tendency to attach simple behavioural labels to species that on detailed examination may be inappropriate. Clear examples of perching and patrolling exist but many species show a wide range of behaviour. All perchers change their location and patrollers stop to feed and it is possible that males are vigilant for mates even on these occasions, as in the case of *L. megera* (cf., Figure 1). *H. semele* (L.) and *M. galathea* among the Satyridae occur at opposite ends of the perching/patrolling spectrum respectively, but *P. tithonus* (L.), *M. jurtina* (L.) and *E. aethiops* (Esper) (Dennis 1982) engage in both activities.

(*To be continued*)